INHERITANCE OF PHOTOPERIOD-INDUCED FLOWERING AND A GLABROUS-STEM MARKER GENE IN *Aeschynomene americana*

BY

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A study of the inheritance of photoperiod-induced flowering and a glabrous/pubescent stem character was conducted on the tropical forage legume *Aeschynomene americana* L. A pubescent, photoperiod-insensitive line and a glabrous, late-flowering, photoperiod-sensitive line were crossed with two pubescent lines, each of which was photoperiod sensitive and flowered at about mid-range. Parents, F_1, F_2, and reciprocal backcrosses of each cross were grown at two Florida locations, Gainesville and Ft. Pierce. Approximately 2000 plants were planted at each location in a randomized complete block design with five replications. Individual plants were classified as pubescent or glabrous, and date of first flowering was recorded. Analysis of the pubescent x glabrous crosses revealed that this trait is controlled at one locus with a glabrous allele completely dominant over a pubescent allele. In crosses of the photoperiod-insensitive parent x the two mid-range, photoperiod-sensitive parents, sensitivity to photoperiod was completely dominant to insensitivity in a one locus, two allele

system. Mather and Jinks's scaling test and method of partitioning components of variation were employed in initial analysis of the crosses between the two mid-range parents and the late flowering line. The data fit an additive-dominance model with most genetic variance being additive. After further analysis with Powers's partitioning method, it was concluded that a completely additive genetic system involving two loci, each with two alleles, was primarily responsible for induction of flowering by photoperiod. Expression appeared to be modified by minor genes and environment.

CHAPTER I
GENERAL INTRODUCTION

Much of the world's crop production is concentrated on a relatively small number of plant species such as wheat, rice, maize, and beans. But as demand for agricultural products increases, the potential contributions of many of the countless other crop plants that are cultivated, including those in the tropics, are being more intensively investigated. Associated with increased interest in evaluation and conservation of cultivated germplasm is the parallel enterprise of collecting and evaluating wild species for potential use as domesticated plants. Most agricultural research has been conducted on temperate climate crops; research on management and improvement of many tropical species is, by comparison, an untouched area of study.

Due to its unique geography and climate, Florida is well suited both for the study of tropical/subtropical plants and for their inclusion in local agricultural production. A good example of this is the forage research presently being carried out in the state. As a major beef producer, Florida grows a substantial amount of forage, making it one of the state's major agronomic crops. Yet the poor nutritive quality of native range and pastures has prompted interest in the possibility of using various exotic tropical plants as forage resources. One such plant is Aeschynomene americana L., also commonly known by its genus name aeschynomene or as American jointvetch.

Aeschynomene is a woody tropical/subtropical legume distributed throughout much of Central and South America as well as the eastern gulf coastal states of the U.S. (24). Although it is considered undomesticated, in Florida the plant is grown as a reseeding annual forage to supplement grass pastures which are of low quality during late summer and fall (9). Aeschynomene's main attributes for Florida are its relatively high nutrient quality, and the fact that it is particularly well adapted to the periodically flooded flatwoods soils that are common in the cattle producing areas of the state (1,9,15). Recognizing the potential of aeschynomene, forage workers have recently begun collecting and evaluating plant introductions from diverse origins, with the objective of developing an improved cultivar.

Development of a cultivar from a wild plant is both exciting for its potential and risky due to the unknown genetic nature of the material. Aeschynomene has many characteristics that show promise for its use as a forage, yet genetic studies are entirely lacking. Although a breeding program does not by any means require genetic definition of every plant character being manipulated, understanding the genetics of some major traits can facilitate development of prudent and efficient breeding plans and thereby help avoid wasted effort. In addition, a knowledge of the genetics of certain characters can aid in defining the genetics of other traits.

Initial characterization of aeschynomene accessions showed a great deal of variation in several traits, including growth habit, plant size, pubescence, flower color, nematode tolerance, and

flowering response to photoperiod (23). The latter is of particular concern in Florida and other subtropical areas where annual fluctuation of daylength can be great. As mentioned, aeschynomene is grown as a reseeding annual; thus ample seed must be produced to establish the subsequent year's crop. However, flowering drastically reduces foliage production, so ideally it must take place as late as possible in the growing season to assure maximum forage yield yet soon enough before the first killing frost to provide the seed necessary for the following year's stand. An understanding of the inheritance of photoperiod induced flowering can aid the breeder in determining if and how he can manipulate this character to maximize forage production.

Another character of interest was the glabrous/pubescent stem. Most aeschynomene lines are pubescent, yet one was distinctly glabrous. While no agronomic benefit can be attributed to either condition, the interest in this character is in its potential value as a marker gene.

After traits of practical importance were identified, the following specific objectives of this research were formulated:

1) Attempt to define the genetics of inheritance of the glabrous/pubescent stem character.

2) Investigate the inheritance of photoperiod-induced flowering in aeschynomene.

CHAPTER II
GLABROUS/PUBESCENT STEM: A SEEDLING MARKER GENE

Introduction

Simply inherited, easily discerned marker genes can be valuable in a variety of genetic studies, ranging from biochemical genetics to practical plant breeding. For the breeder, a seedling marker can be especially useful in that it facilitates early classification of phenotypes, thus eliminating the necessity of growing plants to maturity before evaluation. One objective of our preliminary work on Aeschynomene americana genetics conducted in Florida, was to identify the inheritance of a glabrous/pubescent stem character that appeared to be simply inherited and potentially useful as a seedling marker gene.

Materials and Methods

In 1985 two pubescent accessions identified as 55 and 232 were grown in the greenhouse and crossed with the glabrous accession 206 (Table 2-1). Single F_1 plants, one from each of the two crosses, were grown in the greenhouse, allowed to self-pollinate to set F_2 seed, and were also backcrossed to both of their respective parents. In the summer of 1985 seed from the P_1, P_2, F_1, F_2, BC_{P1}, and BC_{P2} generations of each cross were planted in pet pellets. Three week old seedlings, 15 to 20 cm high, were evaluated for the presence or

Table 2-1. Accessions of *Aeschynomene americana* used as parents.

Accession no.	Phenotype	Origin
55	pubescent	Florida
206	glabrous	Panama
232	pubescent	Brazil

absence of stem pubescence. Next, samples of plants were randomly selected from each generation and planted into the field where they were again observed for pubescence as mature plants of about 150 days age.

Results and Discussion

Seedlings

The definite classification of a seedling as either pubescent or glabrous is difficult until it is about 15 to 20 cm high or at the fifth to seventh node stage of growth. The results of classification at this growth stage are given in Table 2-2.

All offspring arising from self-pollination of the pubescent parent accessions 55 and 232 were pubescent, and all progeny from the selfed glabrous 206 plant were glabrous. The F_1s were all glabrous in both the 55 x 206 and 232 x 206 crosses, evidence that glabrousness is completely dominant. However, in a few plants which were almost completely glabrous, a very few hairs could be seen on the distal ends of some branches, frequently in a row running along the axis of the stem. These plants were noted for the possibility of their constituting an intermediate class.

The F_2 generations of both crosses were observed to segregate rather distinctly into a larger glabrous class and a smaller pubescent class. Again, in evaluation of the F_2, there was some incidence of what appeared to be glabrous plants with a very low level of pubescence. The degree of this was noted as above for the possibility of intermediate classes. When these plants were totaled as an intermediate class, however, the results were inconclusive. When they

Table 2-2. Seedling data and chi-squares of glabrous/pubescent stem character in Aeschynomene americana.

Generation	Pedigree	No. glabrous plants	No. pubescent plants	Observed ratio	Expected ratio	χ^2	P
Parent	55	0	278	no segregation		-*	-
Parent	206	153	0	no segregation		-	-
Parent	232	0	192	no segregation		-	-
F_1	55x206	43	0	no segregation		-	-
F_2	55x206	201	67	201:67	201:67	-	-
BC_{P1}	(55x206)x55	47	49	47:49	48:48	0.042	0.9-0.8
BC_{P2}	(55x206)x206	96	0	no segregation		-	-
F_1	232x206	191	0	no segregation		-	-
F_2	232x206	170	65	170:65	176:59	0.815	0.4-0.3
BC_{P1}	(232x206)x206	75	64	75:64	69.5:69.5	0.870	0.4-0.3
BC_{P2}	(232x206)x232	100	0	no segregation		-	-

*For generations that did not segregate or segregated exactly as expected no chi-square was calculated.

were pooled with the totally glabrous group, there was a 3:1 segregation of glabrous to pubescent. This was true for both the 232 x 206 F_2 and the 55 x 206 F_2; data of the latter cross fit the expected ratio exactly. The data for 232 x 206 also showed a good fit, with a chi-square probability of 0.30 to 0.40.

Backcrosses behaved as expected based on the performance of the F_1 and F_2 generations. In backcrosses to the glabrous parent (55 x 206) x 206 and (232 x 206) x 206, all progeny were glabrous, but in these populations too there were some plants with very low levels of pubescence near the branch tips. The backcrosses to the pubescent parents, (55 x 206) x 55 and (232 x 206) x 232, segregated in a 1:1 ratio, again with some glabrous plants showing some tip pubescence. The (55 x 206) x 55 backcross fit a 1:1 ratio almost exactly. The chi-square for (232 x 206) x 232 also showed good fit, with a probability of 0.30 to 0.40.

Mature Plants

Smaller numbers of mature plants were classified in the field after 150 days to determine if the seedling classification would be similar to that of mature plants. This was found to be so. In the mature plants, those glabrous types with some pubescence by the branch tips were observed more closely than in the seedlings. These plants were then classified as follows: G was completely glabrous; G1 had very few hairs (less than 10) near the tip; and G2 had up to 100 hairs scattered on the branch but still far fewer than a true pubescent type of plant would have. When classified thus, no general trend or

modality was obvious. However, when these subcategories of glabrousness were ignored and all these plants were classified simply as glabrous, very distinct ratios were obvious, just as in the seedling data. The F_1s were all glabrous, and the F_2s segregated at 3:1 glabrous to pubescent. The backcrosses to the glabrous parent were all glabrous and the backcrosses to the pubescent parent segregated at 1:1. Chi-square values and probabilities are listed in Table 2-3.

Conclusion

From the data on both seedlings and mature plants, it appears that there is a simple one gene-two allele system controlling the glabrous/pubescent character, where the glabrous allele, Gl, is completely dominant over the recessive pubescent allele, gl. There does appear to be, however, variable expressivity of this character which results in some plants of the glabrous phenotype having a very slight pubescence, but this is so minimal that it does not interfere with plants being classified simply and quickly as pubescent or glabrous. Therefore, from a practical standpoint, this expressivity should not be a problem in using the glabrous/pubescent character as a marker gene in either seedlings or mature plants.

From a theoretical standpoint, this characteristic is something to ponder. Although there are some other glabrous aeschynomene accessions, they are uncommon (24). Since they are of such low frequency in the specie, they could be termed mutant. Now it is sometimes said that all or most mutations are recessive, yet

Table 2-3. Mature plant data and chi-squares of glabrous/pubescent stem character in Aeschynomene americana.

Generation	Pedigree	No. glabrous plants	No. pubescent plants	Observed ratio	Expected ratio	χ^2	P
F_1	55x206	19	0	no segregation		-	-
F_2	55x206	113	35	113:35	111:37	0.144	0.7
BC_{P1}	(55x206)x55	26	28	26:28	27:27	0.074	0.8-0.7
BC_{P2}	(55x206)x206	74	0	no segregation		-	-
F_1	232x206	50	0	no segregation		-	-
F_2	232x206	108	38	108:38	109.5:36.5	0.082	0.8-0.7
BC_{P1}	(232x206)x206	70	0	no segregation		-	-
BC_{P2}	(232x206)x232	32	43	32:43	37.5:37.5	1.613	0.3-0.2

*For generations that did not segregate or segregated exactly as expected, no chi-square was calculated.

here is an example of a dominant mutant, and it is of low frequency. From our observations, the glabrous plant does not seem to be particularly favored by cattle or insects; herbivory seems identical to that on the pubescent plants. Perhaps geographic isolation has kept the glabrous types from becoming more prevalent, but we have no information on this. One could speculate any number of reasons for glabrousness being uncommon, but nevertheless, its peculiarity lies in its being a dominant mutant allele.

CHAPTER III
INHERITANCE OF PHOTOPERIOD-INDUCED FLOWERING

Introduction

As already outlined in the general introduction, several aeschynomene accessions appeared to be induced to flower by photoperiod. In aeschynomene, as in so many other crops, the timing of flowering can be crucial to yield. To maximize forage production, flowering must be delayed as long as possible, yet still occur at least five weeks before frost to allow ample seed set. To investigate the genetics of flowering, a study employing four parent lines was conducted from 1983 through 1985, culminating in a field experiment at two locations involving approximately 4000 plants.

Literature Review of Photoperiod-Induced Flowering

Since there are virtually no genetic studies published on Aeschynomene, there is little work to refer to for this investigation. On the other hand, studies of the flowering response to photoperiod in other papilionaceous legumes are extensive and can indicate the various modes of inheritance of this character, as well as possible methodologies for experimental design and analysis. Examples of photoperiod induced flowering in Pisum, Phaseolus and Vigna are reviewed below.

Flowering in Pisum

Control of flowering response in Pisum appears to vary from readily identifiable major genes to polygenic systems, depending on the cultivar and environment. Watts et al. employed Jinks's regression of the parent-offspring covariance (Wr) on the variance (Vr) to test the stability of flowering response of Pisum sativum under what he hypothesized as polygenic control (32). He concluded that the genetic system was primarily additive in effect, with dominance insignificant. No major genes were identified.

A similar investigation by Snoad and Arthur (26) utilized seven pea cultivars, which were crossed in a diallel and analyzed by various methods as described by Mather and Jinks (14). Conclusions from these analyses were in agreement that dominance was unimportant in the genetic system controlling flowering. For the cultivars studied, this character appeared to be controlled entirely by a simple additive system.

Snoad and Arthur performed another experiment of similar design but included primitive and wild Pisum accessions in the diallel (27). Since many cultivars may have been developed from a relatively narrow genetic base, this study's inclusion of wild Pisum afforded an opportunity to investigate flowering response in a wider segment of the genome. And, as might be expected, different genetic mechanisms were observed in this set of data. Early flowering resulted from an accumulation of dominant alleles, in contrast to the conclusion reached in the study of seven cultivars mentioned above. Thus, there

was strong evidence of more than one genetic system controlling early flowering in peas.

A more complex genetic system was elucidated by I.C. Murfret (16,17,18). His work identified loci, alleles and their interactions. Relationships involving major genes, dominance, additivity, epistasis, and even pleiotrophy were described. Dominance was definitely important in some systems. Significantly, it was emphasized that what had at first appeared to be quantitatively inherited was actually under qualitative genetic control. Choice of appropriate environmental conditions, large enough populations and following a cross for a number of generations made it possible to recognize and identify major gene systems.

One may conclude from the extent and number of studies of flowering in Pisum that there are a series of genetic systems influencing expression of this character, ranging from quantitative inheritance to identifiable major genes. Therefore, it would be difficult to describe a general genetic model for flowering in the genus, since the hypothesized models frequently vary according to the lineage of the crosses. These genetic systems may indeed be related, but information at this time does not allow for development of a single model that encompasses all described inheritance.

Flowering in Phaseolus

Inheritance of flowering response to photoperiod in beans is similar to that of Pisum in that there seems to be a number of systems ranging from simple inheritance to polygenic (31). And, like peas,

expression of flowering in Phaseolus is sometimes modified by environment.

By using growth chambers, the effect of temperature on flowering response in Phaseolus vulgaris was investigated by Coyne in Nebraska (4). High nighttime temperatures interacted with long photoperiod to greatly delay flowering. Early flowering was found to be determined by a dominant allele in a monogenic system.

In a different set of crosses involving another set of parents, Coyne found expression of flowering response was again affected by temperature. What appeared to be quantitatively controlled at one location showed more obvious modality in a different environment. In the latter, late flowering was found to be controlled by two complementary dominant genes. Such results further illustrate that identification of genetic systems for flowering may be very dependent upon the environmental background of the experiment and that conclusions may hold for only the parents involved in the study, not the whole genome.

Flowering in Vigna

Interaction of temperature and flowering was evident in mungbean, Vigna radiata, which is classified as a short-day plant (30). In a study at Missouri using growth chambers, this interaction was controlled so that the genetics of flowering could be identified in crosses between various plant introductions. A dominant or partially dominant gene for photosensitivity was observed in growth chambers

with photoperiods of 14 hours or greater. It was not expressed in the field at Missouri or at 12 hour photoperiods in the growth chamber.

Summary

A thorough review of the genetics of flowering was presented by Murfret (19), so it is unnecessary to attempt to duplicate that work here. What is of primary interest for our study of aeschynomene is not the specific genetics controlling flowering in other legumes but rather what the trends are. From this brief review of Pisum, Phaseolus, and Vigna we may conclude that with each species there appears to be a number of different genetic systems governing flowering. Generalizations are difficult, and conclusions reached for one set of crosses may not hold true for another, let alone for all members of the species.

Although polygenic or quantitative inheritance was invoked as an explanation of some flowering genetics, there were also a number of major gene systems identified. Since environmental variables, particularly temperature, greatly influence expression of the flowering character, a major gene system could be masked as a quantitative character until adequate environmental background or more sensitive methods of analysis are employed.

Materials and Methods

Four plant introductions of A. americana were selected for use as parents in a series of crosses. These parents were chosen for their collective range of flowering dates at Gainesville, Florida based upon

previous years' observations (Table 3-1). Parent 197 was a very early (long day) flowering plant with an upright, open growth habit and distinctively small, purplish-blue flowers. Two mid-range parents, 55 and 232, were not only similar in flowering date but also in flower color and general growth habit. The fourth parent, P.I. 206 flowered very late at Gainesville and had a procumbent growth habit, glabrous stems and large, yellow-orange flowers.

In December 1983, seeds were scarified with sandpaper and germinated in petri dishes containing moistened filter paper. Seedlings were then transplanted into 15 cm diameter, black plastic pots, each filled with a mixture of 50% potting soil and 50% fumigated field soil. Plants were grown in greenhouses, where they were fertilized and watered as needed. Observations were made for uniformity of phenotype within each P.I., based upon various characteristics such as flower color, plant architecture, pubescence and general appearance. A single plant from each accession was then chosen for use as a parent in crossing. All four parent plants were crossed in a half-diallel, creating six crosses (Table 3-2). Artificial pollinations were made by emasculating the female plant in the late afternoon or evening and pollinating these flowers with donor pollen the next morning. As seeds matured at five to six weeks, they were harvested, bagged and labelled.

In the winter of 1984-85, seed for the backcross and F_2 generations were grown. Seeds of the F_1 were germinated and planted in the manner described above. At least six or more F_1 plants from each cross were observed for various morphological characteristics to

Table 3-1. Aeschynomene accessions used as parents in study of inheritance of photoperiod-induced flowering.

PI no.	Origin	Flowering date at Gainesville based on initial observations	Distinguishing characteristics
55	Florida	Late September	Prolific foliage; upright; pubescent stem; pale yellow flower; yellow pollen
197	Argentina?[+]	Before September	Very open; upright; sparse foliage; pale green; pubescent; very small purple flower; white pollen
206	Panama	November (after frost)	Procumbent; glabrous stem; large yellow-orange flower; yellow pollen
232	Brazil	Early October	Similar to 55

[+] Argentina was our source of germplasm but location of original collection is unknown.

Table 3-2. Half diallel crossing scheme of aeschynomene parents.

	55	197	206	232
55	-	55x197	55x206	232x55
197		-	197x206[+]	232x197
206			-	232x206
232				-

[+] F_1 of 197x206 and the reciprocal 206x197 died as seedlings and so were eliminated from the experiment.

ascertain that they were indeed F_1s and not the result of accidental self-pollination. Then a single F_1 plant was selected from each cross to be backcrossed to its original parents, which had been maintained through the summer. Cuttings of the parents and F_1s were grown to provide additional material for crossing. In addition, the F_1s were allowed to self-pollinate, creating seed for the F_2 generation. Self-pollinated seed was also harvested from each original parent plant for later use in the field. F_1 seedlings from the cross between parents with the most extreme flowering dates, 197x206, died for unknown reasons on three separate plantings. Thus this cross was eliminated from the experiment, leaving five crosses for analysis.

On May 10, 1985, seeds from the P_1, P_2, F_1, F_2, BC_{P1}, and BC_{P2} generations of each cross were scarified and germinated. Seedlings were transplanted three to four days later into commercial peat pellets. When plants were about six weeks old and roots had protruded well through the peat pellets, they were transplanted into the field at two locations, Gainesville and Ft. Pierce, Florida. Gainesville is at approximately 29°N. latitude and Ft. Pierce is at about 27°N. latitude. The soil at the Gainesville site was a well drained Kendrick fine sand (loamy, siliceous, hyperthermic Arenic Paleudult), which was fertilized preplant with 30 kg ha^{-1} of P_2O_5 and 60 kg ha^{-1} K_2O. Plants were set out in an randomized complete block design with five replications. Each replicate was divided into five equal-sized units, one for each of the five crosses. Within each unit P_1, P_2, F_1, F_2, BC_{P1}, and BC_{P2} generations were planted in 16 five-plant rows; that is, each unit contained a family. Each family unit contained one

row of P_1, one row of P_2, two rows of F_1, six rows of F_2, and three rows of each backcross generation. Plants were spaced 1.5 m apart within and between the rows and there were 2 m alleys between units. Irrigation was applied as needed and weeds were controlled by hand. An outbreak of Rhizoctonia was noticed in approximately 15% of the field on about August 12. Benlate was applied twice with a backpack sprayer and once as a drench at the rate of 1 kg ha^{-1}.

The Ft. Pierce location was approximately 320 km south of Gainesville on Florida's Atlantic coast. The soil there was an Oldsmar fine sand (sandy, siliceous, hyperthermic family of Alfic Arenic Haplaquods) and very prone to prolonged flood. Two separate but adjacent fields were planted. Two replications of the experiment were established in a field that had been fertilized and used for growing tomatoes three months earlier. The other three replications were planted in a field that had been in bahia (Paspalum notatum) grass for several years and had not been fertilized. Because of residual fertilizer in the old tomato field, no fertilizer was applied at the Ft. Pierce location. Layout of plants was a duplicate of that at Gainesville. Every plant was observed for the day of the year on which it first flowered; this date was then converted into hours of daylight for that particular day (7). Separate conversions were done for each location to account for the difference in duration of daylight between the two latitudes.

Data that appeared to segregate in distinct classes were analyzed with chi-square goodness-of-fit. Where inheritance appeared quantitative, generation means were analyzed with Mather's scaling

test (13,14). Estimates of broad sense heritability, number of effective factors and components of variance were calculated by Mather and Jinks's partitioning components of variation method (13,14). Powers's partitioning method was employed to further analyze these data (20,21,22). Details of the methods are in the following discussion.

Results and Discussion

Photoinsensitive Allele

After observing the flowering behavior of these parent accessions for two seasons both in the field and in the greenhouse, it became apparent that P.I. 197, initially identified as early flowering, may be uninfluenced by photoperiod, at least under daylength of 14 hours or less. As a six to eight week old plant, this accession was observed to flower in very early July, just after the summer solstice. Plants of the same age grown in the greenhouse flowered in late December, just after the winter solstice. Since these two dates are the maximum and minimum of natural photoperiods, it appears that 197 can flower under any photoperiod after it has reached a certain physiological maturity at about eight weeks of age. Therefore, for the daylength conditions in Florida, this parent may be considered photoperiod insensitive.

Analysis of data

The various generations of crosses between 197 and the two mid-range parents, 55 and 232, were plotted in frequency distributions

with ten-day intervals constituting a class (Tables 3-3 through 3-8). Days of the year rather than hours of daylight were the data analyzed because of our observation that 197 was not induced to flower by daylength, but rather by age of the plant. It was therefore unnecessary to convert the days of the year to hours of daylight.

With the data displayed in such a fashion there appeared to be a definite pattern; this was particularly obvious in the 55 x 197 cross at Gainesville (Table 3-3). The F_1 flowered at the same time as did parent 55, an indication of dominance. In the F_2 there was a flush of flowering at about the same time as the flowering of the 197 parent, then a break, and then a second, larger flush, the majority of which coincided with the flowering of 55. The backcrosses had the same trend, with the backcross to 197 having two definite modes and the backcross to 55 showing no obvious segregation. Similar, but less distinct, patterns were evident in the other frequency distributions.

Based upon these observations, it appeared that a simple major gene system may have influenced flowering in crosses 55 x 197 and 232 x 197. A single gene model having a completely dominant allele, Pr, for photoperiod responsive, and a recessive allele, pr, for photoperiod insensitivity was tested with a Chi-square goodness-of-fit statistic. Classes in the segregating populations were not always perfectly distinct, so they were separated at day 230. All plants flowering before that date were classified as photoperiod insensitive, prpr, and those after that date as photoperiod responsive, PrPr, or Prpr. That particular day was chosen for separating the classes for

Table 3-3. Frequency distributions of generations from 55x197 at Gainesville. Data are numbers of individual plants observed to flower in a given 10-day period.

Gen.	Days of year: 181 190	191 200	201 210	211 220	221 230	231 240	241 250	251 260	261 270	271 280	281 290	291 300	301 310	n	$\bar{X}$	σ^2
P_1 (55)								32	42					74	260.54	8.17
P_2 (197)		39	11											50	200.42	4.41
F_1								15	23					38	261.63	10.67
F_2	1	13	12	-	1	8	7	28	51	13	4	1		139	260.17	687.23
BC_{P1}						5	10	17	32	5				69	258.80	103.13
BC_{P2}		3	29	7	-	-	-	8	13	3	1			64	229.03	850.98

two reasons: it was the latest date at which 197 flowered, and it was frequently where an obvious modal break occurred.

The model was tested for each cross at each location and also for each cross with data from both locations pooled. The pooled tests were run with the idea that larger populations may provide a better sample, and that a primarily Mendelian character should manifest itself the same in two environments that are not greatly dissimilar. Noting that the generation means of the crosses were very similar at both locations, pooling seemed reasonable. When generation means were plotted at each location there was some evidence of genotype by environment interaction (G x E), particularly in the crosses involving 197 (Figures 3-1 through 3-3 and Table 3-9) (12). Even though some means indicated the presence of G x E, conclusions drawn from the pooled data were in agreement with those drawn from individual location data. Thus the G x E was not so great in these two environments that it prevented consistent conclusions from the pooled data.

Most chi-square probabilities for the expected 3:1 PR __ :pr pr of the F_2 generation ranged from .20 to .50 (Table 3-10) (6). The single exception was the 55 x 197 F_2 which had a probability of .05 to .02 when data from both locations were pooled. This is not particularly disconcerting since all of the other 15 segregating generations tested fit the model well. A possible reason for lack of fit may be the arbitrary division of these distributions into ten day classes. It is conceivable that a few pr pr plants could have been classified as Pr __ if they were recorded as flowering on day 231

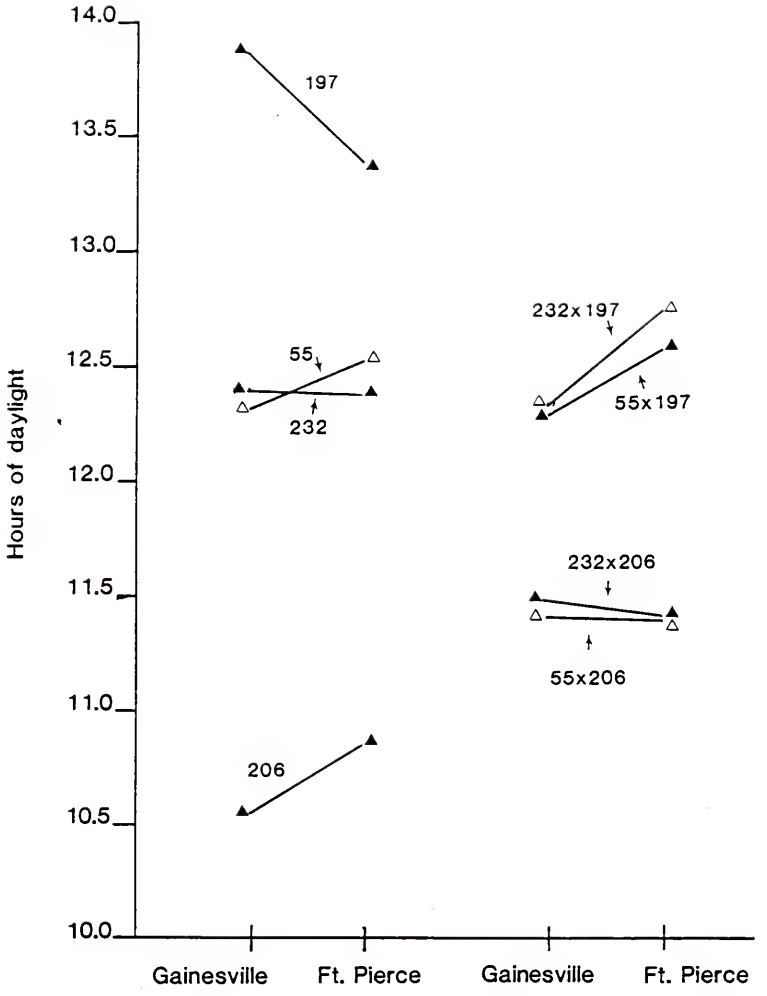

Figure 3-1. Parent and F_1 means at Gainesville and Ft. Pierce.

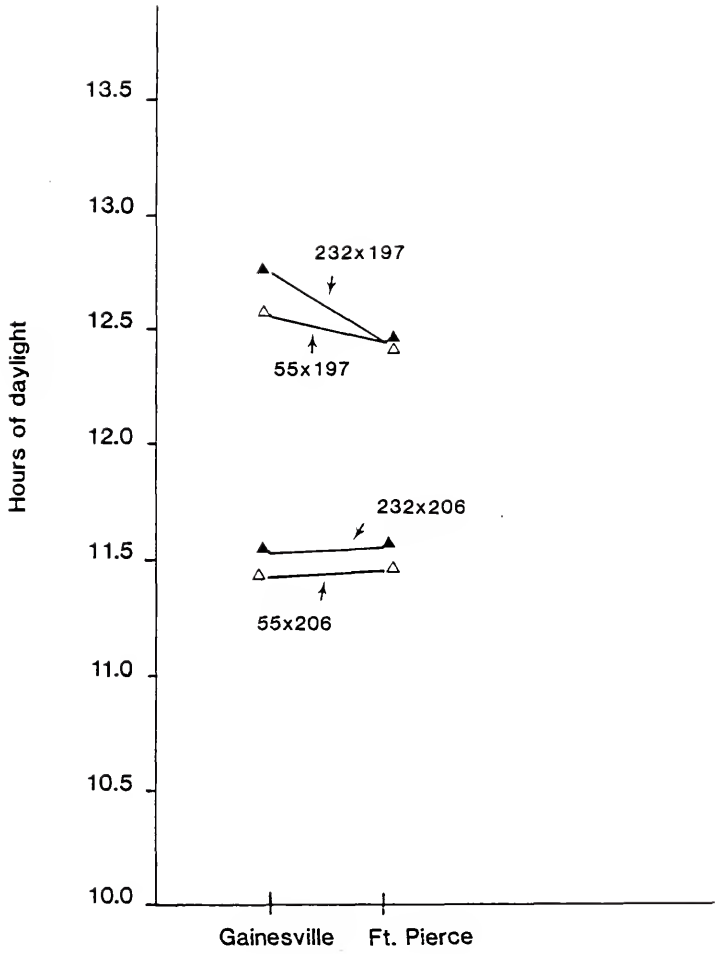

Figure 3-2. F_2 means at Gainesville and Ft. Pierce.

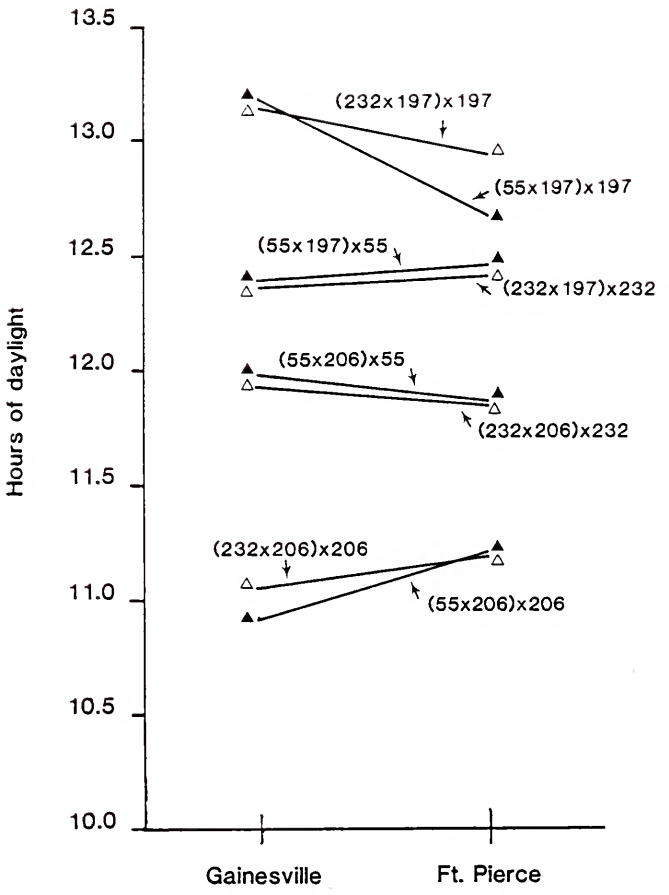

Figure 3-3. Backcross means at Gainesville and Ft. Pierce.

Table 3-4. Frequency distributions of generations from 55x197 at Ft. Pierce. Data are numbers of plants observed to flower in a given 10-day period.

Gen.	Days of year 181 190	191 200	201 210	211 220	221 230	231 240	241 250	251 260	261 270	271 280	281 290	291 300	301 310	n	$\bar{X}$	σ^2
P_1 (55)						7	43	16	5	1	2	1		75	250.61	131.54
P_2 (197)			14	33	3									50	213.22	19.48
F_1							7	16	22	2				47	261.04	57.22
F_2		6	9	8	7	12	12	22	39	27	6			148	252.43	597.76
BC_{P1}				1	4	24	8	4	17	14	3			75	253.17	377.42
BC_{P2}			10	17	1	-	6	7	11	10	5			67	244.16	858.23

Table 3-5. Frequency distribution of generations from 232 x 197 at Gainesville. Data are numbers of plants observed to flower in a given 10-day period.

Gen.	Days of year 181 191 201 211 221 231 241 251 261 271 281 291 301 190 200 210 220 230 240 250 260 270 280 290 300 310	n	$\bar{X}$	σ^2
P_1 (197)	39 11	50	200.42	4.41
P_2 (232)	2 6 39 26 1	74	257.62	36.07
F_1	23 24	47	260.19	14.64
F_2	21 12 1 1 15 3 34 40 5 3 1	136	244.19	755.58
BC_{p1}	12 22 3 - - 1 15 14	67	229.55	841.86
BC_{p2}	6 11 16 30 11 1	75	260.00	128.11

Table 3-6. Frequency distribution of generations from 232 x 197 at Ft. Pierce. Data are numbers of plants observed to flower in a given 10-day period.

	Days of year															
Gen.	181 190	191 200	201 210	211 220	221 230	231 240	241 250	251 260	261 270	271 280	281 290	291 300	301 310	n	$\bar{X}$	σ^2
P_1 (197)			14	33	3									50	213.22	19.48
P_2 (232)						11	21	14	12	10	3	4		75	257.35	276.12
F_1						2	8	17	17	6				50	260.02	91.00
F_2		1	11	11	8	11	12	20	41	25	8	2		150	252.97	572.49
BC_{p1}			15	23	4	4	5	5	12	4	-	2		74	233.66	963.21
BC_{p2}					4	20	3	11	20	16	1			75	255.61	272.89

Table 3-7. Frequency distributions of generations from 55 x 197, data from locations combined.

Gen.	Days of year 181 190	191 200	201 210	211 220	221 230	231 240	241 250	251 260	261 270	271 280	281 290	291 300	301 310	n	$\bar{X}$	σ^2
P_1 (55)						7	43	48	47	1	2	1		149	255.54	94.60
P_2 (197)		39	25	33	3									100	206.82	53.20
F_1							7	31	45	2				85	261.31	36.12
F_2	1	20	20	8	8	20	19	50	90	40	6	5		287	251.34	640.12
BC_{p1}				1	4	29	18	21	49	19	3			144	255.87	252.30
BC_{p2}		3	39	24	1	-	6	15	24	13	2	4		139	236.77	905.78

Table 3-8. Frequency distribution of generations from 232 x 197 with location data combined.

Gen.	Days of year 181 190	191 200	201 210	211 220	221 230	231 240	241 250	251 260	261 270	271 280	281 290	291 300	301 310	n	$\bar{X}$	σ^2
P_1 (197)		39	25	33	3									100	206.82	53.20
P_2 (232)						13	27	53	38	11	3	4		149	257.48	155.87
F_1						2	8	40	41	6				97	260.10	53.47
F_2		22	23	12	9	26	15	54	81	30	11	3		286	248.79	676.48
BC_{p1}		12	37	26	4	4	6	20	26	4	-	2		141	231.71	762.58
BC_{p2}					4	26	14	27	50	27	1	1		150	257.81	204.00

Table 3-9. Generation means in hours of daylight at Gainesville and Ft. Pierce, and test for genotype by environment interaction (G x E).

Generation		Gainesville Mean	Gainesville Std. error	Ft. Pierce Mean	Ft. Pierce Std. error	G x E
		hours of daylight				
Parent	55	12.316	± 0.010	12.534	± 0.034	*
	197	13.872	± 0.005	13.391	± 0.012	*
	206	10.551	± 0.015	10.866	± 0.023	*
	232	12.402	± 0.021	12.360	± 0.049	
F_1	55x197	12.281	± 0.016	12.267	± 0.028	
	55x206	11.399	± 0.058	11.389	± 0.019	
	232x197	12.326	± 0.017	12.293	± 0.035	
	232x206	11.468	± 0.016	11.402	± 0.013	*
F_2	55x197	12.576	± 0.059	12.460	± 0.048	*
	55x206	11.417	± 0.036	11.472	± 0.030	
	232x197	12.471	± 0.062	12.452	± 0.047	*
	232x206	11.547	± 0.039	11.577	± 0.036	
Backcross	(55x197)x55	12.366	± 0.037	12.462	± 0.057	
	(55x197)x197	13.150	± 0.098	12.654	± 0.086	*
	(55x206)x55	11.947	± 0.046	11.853	± 0.064	
	(55x206)x206	10.920	± 0.032	11.224	± 0.028	*
	(232x197)x197	13.133	± 0.094	12.908	± 0.072	*
	(232x197)x232	12.327	± 0.039	12.401	± 0.048	
	(232x206)x206	11.069	± 0.036	11.211	± 0.010	*
	(232x206)x232	11.927	± 0.044	11.852	± 0.047	

*Differences between means were greater than the sum of their standard errors.

Table 3-10. Summary of chi-squares of segregating generations from crosses 55x197 and 232x197.

Generation	Cross	Location	Observed ratio	Expected ratio	χ^2	P
F_2:						
	55x197	Gainesville	27:112	34.75:104.25	2.304	0.2-0.1
	55x197	Ft. Pierce	30:118	37:111	1.760	0.2
	55x197	Loc. combined	57:230	71.71:215.25	4.042	0.05-0.02
	232x197	Gainesville	35:101	34:102	0.039	0.5
	232x197	Ft. Pierce	31:119	37.5:112.5	1.50	0.2
	232x197	Loc. combined	66:220	71.5:214.5	0.564	0.5
Backcross:						
	(55x197)x55	Gainesville	no segregation		-	-
	(55x197)x55	Ft. Pierce	no segregation		-	-
	(55x197)x55	Loc. combined	no segregation		-	-
	(55x197)x197	Gainesville	39:25	32:32	3.062	0.1-0.05
	(55x197)x197	Ft. Pierce	28:39	33:33	2.180	0.2-0.1
	(55x197)x197	Loc. combined	67:64	65.5:65.5	0.069	0.5-0.2
	(232x197)x197	Gainesville	37:30	33.5:33.5	0.731	0.5-0.2
	(232x197)x197	Ft. Pierce	42:32	37:37	1.351	0.5-0.2
	(232x197)x197	Loc. combined	79:62	70.5:70.5	1.050	0.2-0.1
	(232x197)x232	Gainesville	no segregation		-	-
	(232x197)x232	Ft. Pierce	no segregation		-	-
	(232x197)x232	Loc. combined	no segregation		-	-

rather than on 230. Four plants were, in fact, recorded on day 231, and if they had been recorded on day 230, the data would have fit the expected 3:1 at P>.05.

Backcrosses also fit the model well, with no segregation in the backcrosses to the dominant 55 or 232 parents and a 1:1 segregation in backcrosses to the recessive 197 parent. Means of the non-segregating backcrosses were similar to those of the dominant parent and F_1. Probabilities of Chi-squares ranged from about .10 to .50, indicating a good fit between the data and the genetic model.

Although there is substantial evidence to support the contention that a major gene system is involved in controlling flowering in these crosses, it is apparent that other genetic or environmental factors may also influence this behavior. The fact that there was a relatively large range of flowering dates in the parental and F_1 generations indicated that environment could be involved. There is ample evidence that environment, particularly temperature, affects flowering in several legumes (4,10,19), although one would not expect great variation in temperature over a one hectare field. Environmental variability due to flooding, disease, rabbit herbivory, and fertility was observed. Part of the spread in 197 may also be due to disuniform germination, resulting in staggered maturation.

Conclusion

A single locus with a completely dominant and a completely recessive allele appeared to be controlling photoperiod response in these three aeschynomene lines, but there are probably other

environmental and genetic factors influencing this character as well. Different genetic and environmental backgrounds may alter the expression of this gene, as indicated by the G x E observed.

Analysis of Crosses 55 x 206 and 232 x 206

Preliminary analyses

Parents of cross 232 x 55 were too similar in their flowering behavior to provide the variability necessary for genetic evaluation. Therefore this cross was not analyzed and will not be discussed further.

When data from the crosses 55 x 206 and 232 x 206 were displayed in frequency distributions, no obvious modality was observed in the segregating populations, indicating the possibility of quantitative inheritance. Refer to table 3-11 for an example; all other frequency distributions are in Appendix A. The generation means showed a trend for additive gene effects. That is, if genes for a character are primarily additive in effect, the mean of the F_1 should be approximately equal to the average of the means of the two parents. The F_2 mean should be equal to the F_1 mean and the backcross means should be equal to the average of the mean of the respective parent and F_1 (22). When these theoretical means were calculated, they were indeed very similar to the means observed (Tables 3-12, 3-13). From this it could be concluded that one of two possible modes of inheritance was affecting flowering date. The genetics of this character could be quantitative, with a series of minor genes which together have additive effects. This hypothesis of quantitative inheritance would be supported by the lack of obvious modality in the

Table 3-11. Frequency distributions of 55 x 206 generations at Gainesville. Numbers are individual plants per class (cell).

Gen.	Upper class limits in hrs of daylight														n	$\bar{X}$	σ^2
	10.4	10.6	10.8	11.0	11.2	11.4	11.6	11.8	12.0	12.2	12.4	12.6	12.8	13.0			
P_1(55)										9	57	8			74	12.316	0.008
P_2(206	3	32	11	1											47	10.551	0.010
F_1		1	-	1	-	2	16								20	11.399	0.067
F_2	1	4	11	11	18	17	47	14	8	12	5	1			149	11.417	0.190
BC_{P1}							16	7	2	12	13	3			53	11.947	0.112
BC_{P2}		6	28	15	10	10	5								74	10.920	0.077

Table 3-12. Comparison of F_1 and F_2 means with calculated average of parent means.

Cross	Location	F_1	F_2	Avg. of parent means
		---------- hrs of daylight ----------		
55 x 206	Gainesville	11.40	11.42	11.43
55 x 206	Ft. Pierce	11.39	11.47	11.70
55 x 206	Loc. combined	11.39	11.44	11.57
232 x 206	Gainesville	11.47	11.55	11.48
232 x 206	Ft. Pierce	11.40	11.58	11.61
232 x 206	Loc. combned	11.44	11.56	11.55

Table 3-13. Backcross means compared to average of F_1 mean plus parent mean.

Cross	Location					
	Gainesville		Ft. Pierce		Loc. combined	
	BC	$\frac{(F_1+P)}{2}$	BC	$\frac{(F_1+P)}{2}$	BC	$\frac{(F_1+P)}{2}$
	hrs of daylight					
(55x206)x55	11.95	11.86	11.85	11.96	11.90	11.91
(55x206)x206	10.92	10.98	11.22	11.13	11.07	11.05
(232x206)x206	11.07	11.01	11.22	11.13	11.13	11.02
(232x206)x232)	11.93	11.94	11.85	11.88	11.89	11.91

segregating populations. The alternative hypothesis is one of simpler inheritance, where major gene action is additive and gene numbers are very few.

Scaling Test. To further test these ideas, the data were subjected to Mather's scaling test (13,14,28,29). The basis of this test is similar to the ideas just discussed, that the mean of the backcross is equal to the average of the parent and F_1 means, or $BC_1 = 1/2(P+F_1)$. Likewise, the same basis allows for a similar calculation for the F_2 mean. Formulas are given in Table 3-14. If the means perform as predicted in the equation, then their effect is additive on the average, i.e., the additive-dominance model is adequate. It should be emphasized that this does not necessarily mean solely additive gene action; in fact, there will be additive average effects if there is dominance or linkage. Failure of this test implies either that epistasis is a factor and an alternative model is required, or that an alternative scale must be sought to fit the data to the additive-dominance model.

Results of the scaling test were not consistent. At Gainesville, both 55 x 206 and 232 x 206 gave insignificant values for A, B, and C, indicating that the additive-dominance model was appropriate (Tables 3-15, 3-16). However, the Ft. Pierce data yielded three significant t tests, an indication of epistasis or that the scale was not adequate for the model. When the data from both locations were combined, again two tests showed a significant deviation from zero, both in the 232 x 206 cross. But these did so only by a very slight margin and, in fact, are not significant at the .01 probability level. If this were

Table 3-14. Formulas for Mather's scaling test (26, 21).

BC is the symbol for backcross generations.

Subscripts on on $\overline{BC}_1$ and $\overline{BC}_2$ refer to the parent backcrossed to.

P stands for parent.

$\overline{BC} = 1/2\ \overline{P} + 1/2\ \overline{F}_1$

$\overline{F}_2 = 1/4\ (\overline{P}_1+\overline{P}_2+2\overline{F}_1) = 1/2\ \overline{BC}_1 + 1/2\ \overline{BC}_2$

$A = 2\ \overline{BC}_1 - \overline{P}_1 - \overline{F}_1$

$B = 2\ \overline{BC}_2 - \overline{P}_2 - \overline{F}_1$

$C = 2\ \overline{F}_2 - 2\overline{F}_1 - \overline{P}_1 - \overline{P}_2$

$V_A = 4\ V_{\overline{BC1}} + V_{\overline{P1}} + V_{\overline{F1}}$

$V_B = 4\ V_{\overline{BC2}} + V_{\overline{P2}} + V_{\overline{F1}}$

$V_C = 16\ V_{\overline{F2}} + 4\ V_{\overline{F1}} + V_{\overline{P1}} + V_{\overline{P2}}$ +

+ It should be noted that in the reference this formula contains the typographical error "$4\ V_{\overline{F2}}$."

Table 3-15. Mather's scaling test applied to data of cross 55 x 206 to test adequacy of additive-dominance model.

Gainesville	Ft. Pierce	loc. combined
A = 0.179	A = -0.217	A = -0.020
B = -0.110	B = 0.193	B = 0.040
C = 0.003	C = -0.290	C = -0.160
V_A = 0.0114	V_A = 0.0183	V_A = 0.0025
V_B = 0.0372	V_B = 0.0041	V_B = 0.0048
V_C = 0.0343	V_C = 0.0032	V_C = 0.0127
t_A = 1.68	t_A = -1.60	t_A = -0.40
t_B = -0.57	t_B = 3.01**	t_B = 0.58
t_C = 0.02	t_C = -5.12**	t_C = -1.42

*,**$t_{.05}$ = 1.96 and $t_{.01}$ = 2.58 at infinite degrees of freedom.

Table 3-16. Mather's scaling test applied to data of 232 x 206 cross to test adequacy of additive-dominance model.

Gainesville	Ft. Pierce	loc. combined
A = -0.093	A = 0.154	A = 0.110
B = -0.016	B = -0.058	B = -0.040
C = 0.299	C = 0.278	C = 0.270
V_A = 0.0057	V_A = 0.0022	V_A = 0.0025
V_B = 0.0087	V_B = 0.0113	V_B = 0.0048
V_C = 0.0274	V_C = 0.0209	V_C = 0.0127
t_A = -1.23	t_A = 3.28**	t_A = 2.2*
t_B = -0.17	t_B = -0.55	t_B = -0.58
t_C = 1.81	t_C = 1.92	t_C = 2.39*

*,**$t_{.05}$ = 1.96 and $t_{.01}$ = 2.58 at infinite degrees of freedom.

acceptable, the scaling tests would prove the model adequate for both crosses at Gainesville and for both crosses when the data from both locations were combined. The Ft. Pierce data do show significant deviations from zero for B and C of 55 x 206. Since there was good indication that the gene effects are additive in the other data sets, it is likely that the significance of these tests is due to scaling rather than some interallelic interaction.

Partitioning of Components of Variation. Further testing of the data was done using Mather's and Jinks's methods of partitioning components of variation (3,14,28,29). By manipulation of the means and variances of the various generations, it was possible to estimate the genetic and environmental components that make up those variances. Formulas are given in Table 3-17. As the results in Table 3-18 demonstrate, the environmental variance for both crosses was relatively low, meaning that the majority of the total variation was genetic. The dominance component of the genetic variation was negligible, being zero in four of the calculations. Thus most of the genetic variance was additive. Again, additive variance does not necessarily imply additive gene action. But since the genotypic variance was nearly all additive, that is, there was little or no dominance, then we may conclude that genes showed neither dominance nor epistasis (5). Therefore, if there was no or very little dominance or epistasis, then we may also conclude that the gene action was additive.

Table 3-17. Formulae for Mather's and Jinks's partitioning components of variation (21).

Environmental variance	$E = \frac{(V_{P1} + V_{P2} + V_{F1})}{3}$
Dominance variance	$H = 4(V_{BC1} + V_{BC2} - F_2 - E)$
Additive variance	$D = 2(V_{F2} - 1/4\ H - E)$
Genetic variability (broad sense heritability)	$V_G = \frac{(D + H)}{(D + H + E)}$
Number effective factors (loci)	$K_1 = \frac{(P_1 - P_2)^2}{4D}$

Table 3-18. Values for components of variance of crosses 55 x 206 and 232 x 206 using Mather's and Jinks's partitioning method.

Cross	Location	E	H	D	V_G	No. effective factors
55x206	Gainesville	0.028	0	0.324	0.92	2.40
55x206	Ft. Pierce	0.039	0.039	0.078	0.79	8.92
55x206	Loc. combined	0.044	0.030	0.111	0.76	6.66
232x206	Gainesville	0.018	0	0.416	0.96	2.06
232x206	Ft. Pierce	0.071	0	0.186	0.72	3.00
232x206	Loc. combined	0.053	0	0.280	0.84	2.49

Refer to Table 3-17 for definitions of E, H, and D.

Estimates of the number of effective factors, which may be interpreted as the number of loci, were also calculated (Table 3-18). Although there were two high estimates for 55 x 206, most numbers ranged between two and three. If these estimates were at all accurate, then it appears that flowering in aeschynomene may be controlled by a few major genes.

Summary of preliminary tests on data. The results of the tests just discussed showed a definite trend. The means showed additivity both in simple observation and in Mather's scaling test. This additivity was further defined as additive gene action by partitioning the components of variance. And finally, an estimate of the number of effective factors indicated the possibility of a few major genes being responsible for most of the control of this character. All of this evidence leads to a reasonable argument that a major gene model with additive gene action should be tested on the data.

Powers's partitioning method of analysis applied to data

With reasonably strong evidence suggesting that inheritance of flowering response was controlled by a few genes, the data were tested for fit to a two gene model, each locus with two alleles which act additively and with equal effect. Since no obvious modality was observed in the segregating generations' frequency distributions, Powers's partitioning technique was employed to analyze the data. This method of analysis is based on the premise that if the homogeneous populations (parents, F_1) are normally distributed, the effect of environment is normally distributed, since there is no

genetic variability. Lack of normality in the distributions of segregating populations, then, is due to the genetic makeup of the population. Powers envisions populations so distributed as being composed of various genotypes, each of which has its own normal distribution around its own mean. In other words, a few major genes are primarily responsible for control of the character. In contrast, quantitative inheritance would have many genes, each with minor effects, and the resulting distributions would be expected to be normal (11,20,22).

Tests for Normality. The first step in Powers' analysis then is to test for normality in all generations. This is done by creating a theoretical normal distribution from the normal probability table based upon the frequency distributions of the observed data (6). The two distributions are then tested with a chi-square goodness-of-fit statistic. Again, parental and F_1 generations are expected to be normally distributed if they are homogeneous. If major genes are controlling the character under study, the F_2 and backcross generations should not be normally distributed.

F_1 and parent generations. Results of the tests for normality are in Table 3-20. An example of a distribution tested is in Table 3-19; others can be found in Appendix B. In general, the parental and F_1 generations were distributed as expected. Most flowered fairly uniformly, that is, within the range of only a few classes. Following the example of Powers and others, classes with a few outlying plants were combined to get at least ten plants per class (11,20,22,25). Because of the uniformity of flowering and the low number of classes,

Table 3-19. Frequency distributions for 55 x 206 at Gainesville tested for normality. Data are numbers of individual plants observed to flower in a given period of daylight.

	Hrs of daylight															
	10.4	10.6	10.8	11.0	11.2	11.4	11.6	11.8	12.0	12.2	12.4	12.6	12.8	$\bar{X}$	σ^2	n
P_1(55)										9	57	8		12.32	0.008	74
P_2(206)	3	32	11	1										10.55	0.01	47
F_1		1	-	1	-	2	16							11.40	0.067	20
F_2 obs.	1	4	11	11	18	17	47	14	8	12	5	1		11.48	0.19	149
exp.	0	3	6	11	19	25	27	24	17	10	4	2				
BC_{P1} obs.							16	7	2	12	13	3		11.95	0.112	53
exp.							8	10	13	11	7	3				
BC_{P2} obs.		6	28	15	10	10	5							10.92	0.077	74
BC_{P2} exp.		9	15	21	17	9	3									

Table 3-20. Chi-squares of goodness-of-fit test for normality of parent, F_1, F_2, and backcross generations of crosses 55 x 206 and 232 x 206.

	Location					
	Gainesville		Ft. Pierce		Loc. combined	
Entry	χ^2	P	χ^2	P	χ^2	P
55	-*	-	-	-	98.16	<0.001
206	-	-	-	-	-	-
232	-	-	7.38	0.05-0.02	-	-
F_1 55x206	-	-	-	-	-	-
F_1 232x206	-	-	-	-	-	-
F_2 55x206	32.05	<0.001	62.71	<0.001	38.75	<0.001
F_2 232x206	27.44	<0.001	67.18	<0.001	80.84	<0.001
BC_{P1} (55x206)x55	13.06	<0.001	4.95	0.10-0.05	15.81	<0.001
BC_{P2} (55x206)x206	9.51	0.001	-	-	10.09	0.001
BC_{P1} (232x206)x206	4.57	0.10	-	-	2.98	0.3-0.2
BC_{P2} (232x206)x232	16.94	<0.001	12.80	0.01-0.001	37.10	<0.001

*Entries with no values did not have enough degrees of freedom to calculate chi-squares.

degrees of freedom were frequently too few to test the distributions with a chi-square. Thus it may be assumed that since there was a narrow range, the plants in those generations were homogeneous and that any variation was due to environment. In the three parental populations that could be statistically evaluated, one population of 55 had a probability of less than 0.001, indicating a distribution that was not normal. Parent 232 also had one population that had a probability of 0.05 to 0.02, indicating another poor fit. However, the uniformity evidenced in the other parental populations leads me to believe that these deviations from expected behavior were probably due to environmental effects not being normally distributed rather than heterozygosity of the parent genotypes. These two exceptions notwithstanding, evidence clearly demonstrated that the environment was normally distributed.

Segregating generations. For the most part the segregating generations were not normally distributed. All of the F_2 tests had high chi-square values, with probabilities of less than 0.001, but backcrosses were not as consistent in their distribution (Table 3-20). Although most did have high Chi-square values which indicated a lack of normality, there were three backcrosses that had normal distributions. Since the majority were not normal, these may be ignored and further testing of the hypothesis continued.

It may be appropriate at this point to at least question and discuss the assumptions of normality as they apply to this method. Just because a segregating population does or does not fit the normal distribution as it is expected to, must further testing be abandoned?

I think not, partly because of some examples which come to mind. First of all, if a character were controlled by an additive gene system at any number of loci, it seems that the distribution could be normal, rather than abnormal, if alleles had equal absolute effects and broad sense heritability were low (Figure 3-4)(2). For example, a 1:2:1 or 1:4:6:4:1 F_2 segregation could be normally distributed, even when that distribution itself is composed of other normal distributions. Therefore it seems that, in some situations where major genes were suspected, one could accept a normal curve in the F_2 distribution and still be justified to test it. However, since the aeschynomene data sets show little environmental variance and high broad sense heritability, a multi-modal distribution could be expected.

To restate the argument, the point of this example is that distributions of a data set should be interpreted only as an indicator of the type of inheritance. I believe that Powers is often read as stating that homogeneous populations must always be normally distributed and segregating populations must be not normal. But broad sense heritability (i.e., amount of environmental variance) and type of gene action greatly influence the distributions of segregating populations, as illustrated in Figure 3-4. So those distributions which do not conform to these generalities about normality should not necessarily be considered inappropriate for partitioning. Indeed, if major genes are suspected, partitioning may be recommended even if some tests for normality in segregating populations do not perform as predicted. With the aeschnomene flowering data, we hypothesized an

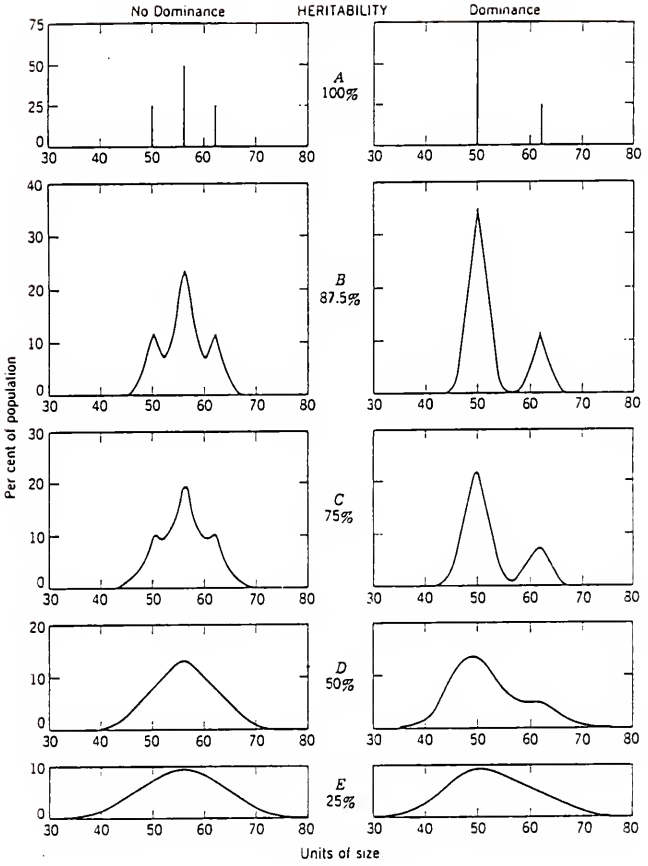

Figure 3-4. Theoretical distributions in F_2. The model postulates monogenic inheritance, and that the effect of environment varies from nil (100 per cent heritability) to the point where environmental effects account for three fourths of the total variability (25 per cent heritability). The left column depicts no dominance; the right column, full dominance.
Source: Allard, R.W. 1960. Principles of plant breeding. John Wiley and Sons, Inc., New York.

additive major gene system with relatively high heritability, so the segregating populations should be abnormally distributed for the most part. However, occasional departures from what is expected may occur due to experimental error. In data sets which demonstrate a clear lack of normality in the homogeneous populations, other iterative methods can be employed (21).

Partitioning of the F_2

Method. With the hypothesized two locus, additive model, the F_2 should segregate into ratios of 1:4:6:4:1. Following Powers's detailed procedure and Sage and Isturiz's example of its application to an additive system, the F_2's of 55 x 206 and 232 x 206 were partitioned into component genotypes (11,21,25). Details of the method can be found in the references, but a general outline of procedure will be presented here. Refer to Tables 3-21 through 3-24 of the 55 x 206 cross at Gainesville as the method is described.

Frequency distributions were created for P_1, P_2, F_1, and F_2 generations (Table 3-11) and then converted to percents (Table 3-21). For example, the ratio 1:4:6:4:1 converted to percents as 6.25:25:37.5:25:6.25. The parental phenotypes therefore should each have made up 6.25 percent of the F_2 population. In this model parent 206 was designated as genotype AABB and parents 55 and 232 as A'A'B'B'. The F_1, then, was of the A'AB'B (two prime) genotype. Since alleles are assumed to have equal effect, all other two prime genotypes (A'A'BB, AAB'B') also had the F_1 phenotype. Therefore the F_1 phenotype made up 37.5 percent of the F_2. When this 37.5 percent and the two parental 6.25 percents were subtracted from the F_2, a 50

Table 3-21. Partitioned F_2 distribution of 55 x 206 at Gainesville expressed as percents.

Population	Genotype	Upper class limits in hrs of daylight												Theoretical %
		10.4	10.6	10.8	11.0	11.2	11.40	11.6	11.8	12.0	12.2	12.4	12.6	
F_2	AABB... A'A'B'B'	0.70	2.70	7.30	7.40	12.10	11.40	31.60	9.40	5.30	8.10	3.10	0.70	100.00
P_2 (206)	AABB	0.40	4.19	1.46	0.13									6.26
F_1	A'A'BB, AA'BB' AAB'B'		1.88	-	1.88	-	3.75	30.0						37.50
P_1 (55)	A'A'B'B'									0.76	4.81	0.68		6.25
Residual	A'A'B'B, AA'B'B' A'ABB, AAB'B	0.30	5.84	5.39	12.1	7.65	1.60	9.40	4.56	3.29	2.42	0.70		50.00

Table 3-22. Theoretical distribution of residual genotypes from partitioned 55 x 206 F_2 expressed as percents.

Genotype	Class centers in hrs of daylight												Total %	SX	$\bar{X}$	σ^2	σ
	10.3	10.5	10.7	10.9	11.1	11.3	11.5	11.7	11.9	12.1	12.3	12.5					
A'ABB, AAB'B	0.30	-3.37	5.84	5.39	12.10	3.83	0.80						24.89	275.73	11.08	0.0450	0.2121
A'A'B'B, AA'B'B'						3.83	0.80	9.40	4.54	3.29	2.42	0.7	24.98	294.81	11.80	0.0408	0.2020

Single prime allele (A'ABB, AAB'B)

$$m = \frac{\sigma^2_{F_1} - \sigma^2_{206}}{\bar{X}_{F_1} - \bar{X}_{206}} = \frac{0.067-0.010}{11.40-10.55} = 0.067$$

$$b = \sigma^2_{206} - (m * \bar{X}_{206})$$
$$= 0.010-(0.067*10.55)$$
$$= -0.6974$$

$$y = mx + b$$
$$= 0.067\ (11.08)+(-0.6974)$$
$$= 0.045$$

Three prime alleles (A'A'B'B, AA'B'B')

$$m = \frac{\sigma_{F_1} - \sigma^2_{55}}{\bar{X}_{F_1} - \bar{X}_{55}} = \frac{0.067-0.008}{11.40-12.32} = -0.064$$

$$b = \sigma^2_{55} - (m * \bar{X}_{55})$$
$$= 0.008-(-0.064*12.32)$$
$$= 0.796$$

$$y = mx + b$$
$$= (-0.064*11.80)+0.796$$
$$= 0.0408$$

Table 3-23. Theoretical F_2 distribution of 55 x 206 at Gainesville built from theoretical frequency distributions of component genotypes.

Population	Genotype	Upper class limits in hrs daylight												Theor.
		10.4	10.6	10.8	11.0	11.2	11.4	11.6	11.8	12.0	12.2	12.4	12.6	%
206	AABB	6.38	68.09	23.40	2.13									6.25
One prime allele	A'ABB, AAB'B	0.07	1.12	8.15	29.63	32.59	21.88	5.84	0.68					25.00
F_1	A'A'BB, A'AB'B, AAB'B'		5.0	0	5.0	0	10.0	80.0						37.50
Three prime alleles	A'A'B'B, AA'B'B'					0.15	2.24	13.72	33.89	33.89	13.72	2.24	0.15	25.00
55	A'A'B'B'										12.16	77.02	10.81	6.25
F_2	AABB...A'A'B'B'	0.42	6.41	3.50	9.42	8.19	9.78	34.89	8.64	8.47	4.19	5.37	0.71	100

Table 3-24. Chi-square contingency table of 55 x 206 at Gainesville.

Class center in hrs daylight	Observed	Expected	Theoretical	$\frac{(O-E)^2}{E}$
10.3	1	0.82	0.63	
10.5	4	6.78	9.55	0.0057
10.7	11	8.11	5.22	
10.9	11	12.52	14.04	0.1845
11.1	18	15.1	12.20	0.5569
11.3	17	15.79	14.57	0.0927
11.5	47	49.49	51.98	0.1253
11.7	14	13.43	12.87	0.0242
11.9	8	10.31	12.62	0.5175
12.1	12	9.12	6.24	
12.3	5	6.5	8.00	0.1095
12.5	1	1.03	1.06	
				1.6163

1/2 χ^2 = 1.6163 χ^2 = 3.2326 df = 5 P = 0.70 to 0.50

percent residual made up of the A'ABB, AAB'B (single prime) and A'A'B'B, AA'B'B' (triple prime) genotypes remained. Single prime and triple prime genotypes each made up 25 percent of the F_2.

To obtain actual values for the residual distribution, parent, F_1 and F_2 distributions were converted to percents within each class or cell of the distribution. For example, the distribution of the 206 parent was converted to percents so that the sum of all cells of the distribution equaled 6.25. The same was done for the other generations. Then the F_1 and parent distributions were subtracted from the F_2, leaving a residual distribution that had percents in each cell, which in total equaled 50.

The residual distribution was then partitioned into its two component distributions, one for single prime genotypes A'ABB, AAB'B and one for triple prime genotypes A'A'B'B, AA'B'B' (Table 3-22). The assumption was that those entries falling on one side of the F_1 mean were of the single prime genotypes and those on the other side had triple prime genotypes. Since the classes were arbitrary, tails of the two distributions could fall into the same cells. Hence the values in the two cells on either side of the F_1 mean were divided equally between the two distributions.

Next means and variances were calculated for these theoretical distributions using the formula $y = mx + b$. The resulting parameters were necessary to construct theoretical normal curves for both the single prime and triple prime genotypes. To do so, means were subtracted from the higher value of each cell and divided by the standard deviation, i.e., the usual procedures for building normal

curves from means and variances. These values were then looked up in a normal probability table and the percentages entered into a theoretical distribution containing all possible genotypes (6) (Table 3-23). Note that in this table frequencies for each cell of the parent and F_1 distributions were converted to percentages.

Finally a theoretical F_2 was created by multiplying the individual cell frequencies of each genotype by the genotype's theoretical percentage. For example, if cell 10.8 had a frequency of 23.40 percent for the parent 206 genotype, AABB, then 23.40 was multiplied times 6.25 percent, the theoretical percent of the F_2 made up of the 206 genotype. The same procedure was repeated for each distribution with an entry in the 10.8 cell. These values were then summed and entered as the percent of the theoretical F_2 that fell into that particular cell.

Theoretical F_2 distributions so constructed were then tested for homogeneity against the observed F_2 using a Chi-square statistic. A contingency table was built by dividing the total number of F_2 observations by 100 and multiplying this number by the percent in each class of the theoretical F_2 (Table 3-24). These calculations gave a theoretical number of plants for each class. A subtotal of the observed plus theoretical values for each class was calculated and divided by two, producing the expected value for each class to be tested against the observed. As in the test for normality, outlying individuals in the tails were pooled until the last cell contained at least ten plants.

Degrees of freedom in contingency tables are calculated as (rows-1) (columns-1). But since means were calculated for the two theoretical distributions of A'ABB, AABB' and A'A'B'B, AA'B'B', two more degrees of freedom were lost. So the final degrees of freedom was equivalent to n-3 where n equaled the number of classes.

Both the observed and the theoretical values had to be tested against the expected. Since the expected values were half way between the observed and theoretical, testing the observed against the expected and multiplying the resulting chi-square by two gave the same result as separately testing both the observed and theoretical separately.

It is not clear to me why Powers chose to test the data with a Chi-square test for homogeneity rather than a goodness-of-fit test. In building and testing the contingency table, the expected is half-way between the observed and theoretical values, which, of course, favors a good fit. While the procedure is correct, the appropriateness of its application to this type of data has not been justified in the references that I have followed or criticized in discussion of the method (8). So, even though I do question the method, I have employed it exactly as described by the authors.

Results of F_2. Chi-square probabilities listed in Table 3-25 demonstrated that the genetic model fits the data fairly well. Contingency tables and calculations are in Appendix C. All probabilities were 0.05 or greater except for 232 x 206 at Gainesville. When the tails of the distribution were combined to give ten or more plants per cell, the calculated Chi-square of this cross

had a probability of <0.01. The lack of fit cannot be attributed to inadequate scale because the data for 232 x 206 at Gainesville tested satisfactorily in Mather's scaling test (Table 3-16). Epistasis can also be ruled out if we accept the scaling test conclusion that the additive-dominance model was adequate. The data also were distributed as expected in tests for normality. We might then conclude that the flowering dates for this cross at Gainesville were slightly more affected by errors in taking data or environment, and thus did not have the background to fully reveal the genetically controlled behavior.

The relatively high probabilities of the other five data sets were strong evidence that flowering response to photoperiod in crosses 55 x 206 and 232 x 206 was primarily under the genetic control of two loci, each with two alleles with additive gene action. It should be emphasized that these two major loci appear to be a predominant genetic feature but by no means the sole factor affecting induction of flowering. To further test the model analysis was done on backcross data.

Partitioning the Backcrosses

Method. The general procedure for the backcross analysis was the same as that of the F_2. Again the hypothesized genetic model was that 206 was of genotype AABB, 55 and 232 were A'A'B'B', and that each of the four alleles had equal absolute effect with additive gene action. Using Tables 3-26 and 3-27 of the (232 x 206) x 206 backcross at Gainesville as an example, one can see that plants were expected to segregate phenotypically in a 1:2:1 or 25:50:25 percent ratio. In

other words 25 percent should be of the 206 parental genotype AABB; 25 percent should be of the F_1 AA'BB' genotype; and 50 percent should have single prime genotypes A'ABB or AAB'B (Table 3-26). In the backcross to the 232 parent, ratios were identical but the genotypes were 25 percent A'A'B'B'; 25 percent A'AB'B; and 50 percent triple prime A'A'B'B or AA'B'B'. Since the 50 percent group was theoretically unlike either the parent or F_1 in genotype, it made up the residual frequency distribution, which was then used in creating the theoretical backcross distribution.

Testing of the observed backcross frequencies against the theoretical was done the same as in testing the F_2. The one difference was that since only one set of parameters was calculated for each backcross, degrees of freedom were equivalent to n-2. Again tails were combined until they had data from at least ten plants (Table 3-28).

Results of backcrosses. At first glance the backcross data did not support the proposed hypothesis quite as definitively as did the F_2. As can be seen in the summary of backcross Chi-squares in Table 3-29, there were six tests that fit the genetic model. These results lend strong support to the conclusion reached after analysis of the F_2 that the gene model was adequate. However, there were also six backcrosses with $P = <0.01$, indicating lack of homogenity.

Two main reasons may be suggested as causes of poor fit between the observed and theoretical data in those six backcrosses. One is cell size which is compounded by environmental effects. Although there appears to be a major gene system at work, there are also other

Table 3-25. Chi-squares of test for homogeneity between F_2 data and theoretical distributions.

Cross	Location	Chi-square	Probability
55x206	Gainesville	3.23	0.70 to 0.50
55x206	Ft. Pierce	7.22	0.10 to 0.05
55x206	Loc. combined	12.02	0.10 to 0.050
232x206	Gainesville	16.30	<0.01
232x206	Ft. Pierce	6.13	0.20 to 0.10
232x206	Loc. combined	12.03	0.20 to 0.10

Table 3-26. Partitioned frequency distribution of (232 x 206) x 206 at Gainesville expressed as percents.

Population	Genotype	Upper class limits in hrs of daylight								Theoretical %
		10.4	10.6	10.8	11.0	11.2	11.4	11.6	11.8	
BC_{P1}	AABB... AAB'B'		5.63	18.31	21.31	18.31	16.90	19.72		100.00
P_1 (206)	AABB	1.60	17.02	5.85	0.53					25.00
F_1	AAB'B', A'AB'B A'A'BB						7.0	15.00	3.00	25.00
Residual	A'ABB,	-1.60	-11.39	12.46	20.60	18.31	9.90	4.72	-3.00	50.00

Table 3-27. Theoretical frequency distribution of (232 x 206) x 206 at Gainesville built from theoretical frequency distributions of component genotypes.

Population	Genotype	Upper class limits in hrs of daylight								Theoretical %
		10.4	10.6	10.8	11.0	11.2	11.4	11.6	11.8	
P_1 (206)	AABB	6.38	68.09	23.40	2.13					25.00
F_1	Any two prime alleles						28.00	60.00	12.00	25.00
Residual	Any one prime allele			0.17	13.39	63.16	22.76	0.51		50.00
BC_{P1}	AABB... AAB'B'	1.60	17.02	5.94	7.23	31.58	18.38	15.26	3.00	100.00

Table 3-28. Chi-square contingency table for (232 x 206) x 206 at Gainesville.

Class center in hrs daylight	Observed	Expected	Theoretical	$\frac{(O-E)^2}{E}$
10.3	0	0.57	1.14	
10.5	4	8.04	12.08	0.0028
10.7	13	8.61	4.22	
10.9	15	10.07	5.13	2.4136
11.1	13	17.71	22.42	1.2525
11.3	12	12.53	13.05	0.0224
11.5	14	12.42	10.83	
11.7	0	1.06	2.13	0.0201
				3.7115

1/2 χ^2 = 3.7115 χ^2 = 7.423 df = 3 P = 0.10 to 0.05

factors, probably both genetic and environmental, which blur the effects of the major genes. That environment can affect expression of major genes controlling photoperiod induced flowering is well established (3,10,17,19). It is conceivable then that plants with similar but different genotypes such as A'AB'B and A'ABB may occasionally be classed as the same phenotype (that is, they may fall into the same cell) if some other factor has blurred the distinction between the two. Distributions could have been influenced by environmental conditions such as Rhizoctonia, herbivory by rabbits, flooding, and soil fertility, which were observed in localized areas of the experiment. Larger populations or more and smaller cells in the frequency distribution may facilitate partitioning and minimize the effect of these factors.

A second suggestion as to the cause of poor fit in these six backcrosses is that the total range of the parents is too narrow. Backcrosses by definition are narrower in range than the F_2 and contain fewer genotypes. All genotypes lie between the F_1 and the parent. For example, possible genotypes in (55x206)x206 are AABB, A'AB'B, and A'ABB or AAB'B. The latter genotypes, A'ABB and AAB'B, differ from the parent and F_1 by only one allele. If the effect of each allele is slight, the effects of environment or minor genes may blur the distinction between phenotypes. If two parents represented the two extremes of the character under study, the effects of these alleles would be greater and classifications would be easier. But these aeschynomene accessions used as parents represented perhaps less

Table 3-29. Chi-squares from test of homogeneity between backcross data and theoretical distributions.

Cross	Location	Chi-square	Probability
(55x206)x55	Gainesville	14.14 (1.20)	<0.01 (0.70 to 0.50)
(55x206)x55	Ft. Pierce	3.12	0.70 to 0.50
(55x206)x55	Loc. combined	24.89 (7.73)	<0.01 (0.10)
(55x206)x206	Gainesville	0.93	0.50 to 0.30
(55x206)x206	Ft. Pierce	0.57	0.50 to 0.30
(55x206)x206	Loc. combined	2.79	0.30 to 0.20
(232x206)x206	Gainesville	7.42	0.10 to 0.05
(232x206)x206	Ft. Pierce	11.05	<0.01
(232x206)x206)	Loc. combined	3.39	0.50 to 0.30
(232x206)x232	Gainesville	16.29 (2.58)	<0.01 (0.20 to 0.10)
(232x206)x232	Ft. Pierce	18.81 (12.46)	<0.01 (0.05 to 0.01)
(232x206)x232	Loc. combined	16.41 (4.41)	<0.01 (0.20 to 0.10)

Note: Chi-squares and probabilities in parentheses are calculated by combining two adjacent cells to account for environmental error. See text for discussion.

than half the observed range of initiation of flowering. Greater variation would facilitate a more conclusive backcross analysis.

Some examples taken from Tables 3-30 through 3-33 can be used to illustrate how environmental factors may have resulted in some backcrosses failing the homogeneity test. It is interesting to note that in four of the six backcross distributions that did not fit the model, very low observed values were in cells with class center 11.9, and higher than expected values were observed for cells with class center 11.7. The low values in 11.9 resulted in high Chi-squares for those cells and the subsequent failure of the observed distribution to fit the theoretical. But if values in cells 11.9 and 11.7 were combined, Chi-squares were greatly reduced and, in fact, three of those four distributions would statistically fit the theoretical (see values in parentheses Table 3-29). Only (232 x 206)x232 at Ft. Pierce did not and then just barely with a P = 0.05 to 0.01. It is conceivable that some environmental factor occurring at the daylength period around 11.9 hours delayed flowering in several plants so that they fell into the 11.7 cell. These daylengths occurred during the first fifteen days of October, a time of year known to have erratic and variable weather. Of course, weather conditions would be equal over the general area of a one hectare field, and not so localized as to affect one area differently than another. But weather conditions interacting with minor genes of some segregants or compounding other environmental factors such as flooding could quite possibly affect the physiology of flowering, causing a delay. Therefore the combining of

Table 3-30. Chi-square contingency table for (232 x 206) x 232, data from locations combined.

Class center in hrs daylight	Observed	Expected	Theoretical	$\frac{(O-E)^2}{E}$
10.9	0	0.005	0.01	
11.1	0	0.08	0.16	1.3228
11.3	12	16.62	21.23	
11.5	35	29.80	24.60	0.9074
11.7	35	28.93	22.86	1.2735
11.9	8	17.23	26.46	4.9444 (0.2163)+
12.1	19	19.15	19.31	0.0012
12.3	22	18.56	15.12	0.6376
12.5	12	11.02	10.04	
12.7	5	5.78	6.56	
12.9	0	1.38	2.76	0.0248
13.1	1	0.5	0	
				8.2043

Combined classes:
$1/2\ \chi^2 = 8.2043$ $\chi^2 = 16.4085$ df = 5 P = <0.01

+Combined classes 11.7 and 11.9:
$1/2\ \chi^2 = 2.2027$ $\chi^2 = 9.4054$ df = 3 P = 0.20 to 0.10

Table 3-31. Chi-square contingency table for (232 x 206) x 232 at Gainesville.

Class center in hrs daylight	Observed	Expected	Theoretical	$\frac{(O-E)^2}{E}$
11.3	2	3.60	5.19	
11.5	18	14.94	11.87	0.1166
11.7	18	14.32	10.63	0.9457
11.9	2	10.44	18.88	6.8231 (0.9151)+
12.1	12	11.08	10.15	0.0764
12.3	15	11.89	8.77	
12.5	6	6.25	6.51	
12.7	0	0.63	1.25	0.1808
12.9	0	0.38	0.75	
13.1	1	0.50	0	
				8.1426

Combined classes:
1/2 X^2 = 8.1426 X^2 = 16.2852 df = 3 P = 0.001

+Combined classes 11.7 and 11.9:
1/2 X^2 = 1.2889 X^2 = 2.5778 df = 2 P = 0.20 to 0.10

Table 3-32. Chi-square contingency table for (232 x 206) x 232 at Ft. Pierce.

Class center in hrs daylight	Observed	Expected	Theoretical	$\frac{(O-E)^2}{E}$
11.3	10	12.34	14.67	0.4437
11.5	17	11.44	5.87	2.7022
11.7	17	15.91	14.82	0.0747
11.9	6	14.31	22.62	4.8257 (1.7250)+
12.1	7	5.76	4.51	0.2683
12.3	7	4.75	2.50	1.0658
12.5	6	4.38	2.75	
12.7	5	5.13	5.25	0.0238
12.9	0	1.00	2.00	
				9.4042

Combined classes:
$1/2\ X^2 = 9.4042$ $X^2 = 18.8084$ df = 5 P = <0.01

+Combined classes 11.7 and 11.9:
$1/2\ X^2 = 26.2288$ $X^2 = 12.4576$ df = 4 P = 0.05 to 0.01

Table 3-33. Chi-square contingency table for (55 x 206) x 55 at Gainesville.

Class center in hrs daylight	Observed	Expected	Theoretical	$\frac{(O-E)^2}{E}$
10.5	0	0.33	0.66	
10.7	0	0	0	
10.9	0	0.33	0.66	0.1283
11.1	0	0	0	
11.3	0	0.67	1.33	
11.5	16	13.3	10.6	
11.7	7	3.66	0.32	3.0479
11.9	2	6.83	11.66	3.4157 (0.2143)+
12.1	12	13.74	15.48	0.2203
12.3	13	11.88	10.75	
12.5	3	2.22	1.43	0.2589
				7.0711

Combined classes:
1/2 χ^2 = 7.0711 χ^2 = 14.1422 df = 3 P = 0.01 to 0.001

+Combined classes 11.7 and 11.9:
1/2 χ^2 = 0.6015 χ^2 = 1.203 df = 2 P = 0.70 to 0.50

two adjacent cells may be justified in order to overcome this environmentally caused error.

If this proposition is acceptable it could also be applied to (55 x 206)x55 data in Table 3-34 for cells 11.3 and 11.5. Pooling these two classes results in a Chi-square probability of 0.10. Since cells 11.3 and 11.5 occurred about October 16 through October 25, it is quite possible this backcross was affected by environment in a manner similar to that described above. Accounting for this source of error then would result in eleven of the twelve backcross populations supporting the model.

Attempts to explain the poor fit of some of the backcrosses should not be construed as an attempt to make the data conform to a preconceived idea. There is considerable evidence from the F_2 and other backcrosses that the model is plausible. It is imperative, then, to look for possible reasons why certain segregating populations behaved differently than expected. Acknowledging some of the possible sources of error described above, it can be concluded that, as a whole, the backcross data support the hypothesized genetic model.

Summary. Initial observations of the generation means of crosses 55 x 206 and 232 x 206 indicated that genes controlling photoperiod induced flowering were additive in effect. Testing the data with Mather's scaling test supported this contention; most tests showed the additive-dominance model was adequate. Further testing revealed little or no dominance variance and suggested that the number of effective factors was two or three. Hence it seemed reasonable to propose that inheritance of flowering in these crosses might be

Table 3-34. Chi-square contingency table for (55 x 206) x 55 data from locations combined.

Class center in hrs daylight	Observed	Expected	Theoretical	$\frac{(O-E)^2}{E}$
10.3	0	0.28	0.55	
10.5	0	0	0	
10.7	0	0.28	0.55	3.2480
10.9	0	0.28	0.55	
11.1	0	5.30	10.61	
11.3	10	11.41	12.82	
11.5	21	12.74	4.47	5.3534 (0.0166)
11.7	17	14.84	12.67	0.3144
11.9	6	11.91	17.82	2.9327
12.1	18	15.49	12.97	0.4067
12.3	16	14.64	13.28	0.1263
12.5	8	7.38	6.75	
12.7	2	3.07	4.14	0.6810
12.9	0	0.41	0.82	
				12.4436

Combined classes:
$1/2\ \chi^2 = 12.4436$ $\chi^2 = 24.8872$ df = 5 P = <0.01

With 11.5 combined:
$1/2\ \chi^2 = 3.8653$ $\chi^2 = 7.7306$ df = 4 P = 0.10

controlled at two loci, each with two alleles and all alleles acting additively with equal absolute effect. The late flowering parent 206 was designated AABB. Parents 55 and 232, which both flowered in late mid-season, were designated A'A'B'B'.

Since segregating generations showed no obvious modality, Powers's partitioning method was used to test the genetic model. F_2 data sets fit the model well in five of the six analyses performed. Chi-square probabilities were generally in the 0.20 to 0.30 range. Backcrosses also supported the model in half of the data sets analyzed. Since most evidence fit the model, it was suspected that the six backcrosses that did not fit were affected by minor genetic or environmental effects, small populations, flowering dates of the parents being too similar, and the arbitrary nature of the frequency distribution cells. Minor manipulation of the data resulted in eleven of twelve backcrosses tested fitting the model. Despite the fact that some analyses did not support the hypothesis, the majority of the evidence demonstrates that flowering in these two crosses is controlled primarily by an additive genetic system with two loci, each with two alleles of equal effect.

CHAPTER IV
CONCLUSION

In this study the genetics controlling stem pubescence and photoperiod-induced flowering were examined. The interest in stem pubescence lies in its potential use as a marker gene which is detectable in seedlings. Evidence from crosses between one glabrous and two pubescent parents showed that this trait is governed by two alleles at one locus. Glabrousness, Gl _, is dominant over pubescence, gl gl. With such simple inheritance and easily classified phenotypes, the glabrous trait can be readily incorporated into other genetic backgrounds and employed in further genetic studies.

The genetics of the effect of photoperiod on flowering induction appeared to involve two separate genetic systems. At one level was the responsiveness (or lack of it) to photoperiod. The F_2 generations from crosses between two photoperiod responsive genotypes and a photoperiod insensitive genotype segregated in a 3:1 ratio of photoperiod responsive to insensitive, indicating complete dominance at one locus. The backcross data confirmed this. Thus, responsiveness to photoperiod appeared to be controlled by a dominant allele Pr and the lack of photoperiod response was conditioned by the homozygous recessive pr pr genotype. Although there was clearly a major gene system involved in expression of this trait, the breadth of each class in the segregating generation indicated that other minor genetic factors or environment may also affect flowering.

At the second level was the genetics controlling those genotypes that were photoperiod responsive. Means and variances of segregating generations from crosses between mid-range and late flowering parents indicated additive gene action. Further analysis demonstrated that two loci, each with two alleles, controlled the initiation of flowering as induced by duration of daylight. Although there was no clear division of classes, due in part to the limited range of the parents involved, partitioning analysis indicated that the data fit an additive gene model and that all four alleles had equal effect. Even though there appeared to be a major genetic system, minor genes and environment surely modify its expression.

It should be emphasized that the conclusions reached in this study are only for the accessions involved. While the identified genetics apply to other aeschynomene lines, by no means is it implied that inheritance of photoperiod response is limited to these genetic systems. As is so frequently demonstrated in other studies of this trait, several additional genetic mechanisms may be identified from other sources of germplasm.

Because environment, particularly temperature, frequently modifies genetic expression of flowering, a study using growth chambers could help define this interaction. Although the data generated in this experiment yielded fairly well defined conclusions, the presence of an environmental effect was evident. Controlled temperature and exposure to light could help clarify the relationship between environment and genetics and how they affect flowering in aeschynomene.

APPENDIX A
FREQUENCY DISTRIBUTIONS OF 55 x 206 AND 232 x 206

Table A-1. Frequency distributions of 55 x 206 generations at Ft. Pierce.

Gen.	Upper class limits in hrs of daylight														n	$\bar{X}$	σ^2
	10.6	10.8	11.0	11.2	11.4	11.6	11.8	12.0	12.2	12.4	12.6	12.8	13.0	13.2			
P_1(55)						3	-	1	4	6	31	25	5		75	12.534	0.086
P_2(206)		6	36	3											45	10.866	0.023
F_1				1	17	6									24	11.389	0.009
F_2			5	30	62	18	10	7	6	6	5				149	11.472	0.139
BC_{P1}					10	5	10	4	6	3	5	2			45	11.853	0.187
BC_{P2}		2	12	16	37	-	2	-	-	1					70	11.224	0.055

Table A-2. Frequency distributions of 232 x 206 generations at Gainesville.

Gen.	Upper class limits in hrs of daylight														n	$\bar{X}$	σ^2
	10.4	10.6	10.8	11.0	11.2	11.4	11.6	11.8	12.0	12.2	12.4	12.6	12.8	13.0			
P_1(206)	3	32	11	1											47	10.551	0.010
P_2(232)									1	7	32	26	5	3	74	12.402	0.032
F_1						14	30	6							50	11.468	0.013
F_2		3	6	10	10	31	33	11	7	15	16	3			145	11.547	0.226
BC_{P1}		4	13	15	13	12	14								71	11.069	0.094
BC_{P2}						2	18	18	2	12	15	6	-	-	74	11.927	0.145

Table A-3. Frequency distributions of 232 x 206 generations at Ft. Pierce.

Gen.	Upper class limits in hrs of daylight														n	$\bar{X}$	σ^2
	10.4	10.6	10.8	11.0	11.2	11.4	11.6	11.8	12.0	12.2	12.4	12.6	12.8	13.0			
P_1(206)			6	36	3										45	10.866	0.023
P_2(232)						4	1	3	7	10	10	11	21	8	15	12.360	0.180
F_1						35	13								48	11.402	0.009
F_2			1	3	13	57	23	17	7	7	9	7	1		145	11.57	0.164
BC_{P1}				7	31	23	3								64	11.211	0.023
BC_{P2}						10	17	17	6	7	7	6	5		75	11.852	0.167

Table A-4. Frequency distributions of 55 x 206 generations, location data combined.

Gen.	Upper class limits in hrs of daylight														n	$\bar{x}$	σ^2
	10.4	10.6	10.8	11.0	11.2	11.4	11.6	11.8	12.0	12.2	12.4	12.6	12.8	13.0			
P_1(55)							3	-	1	13	63	39	25	5	149	12.425	0.058
P_2(206)	3	32	17	37	-	3									92	10.705	0.041
F_1		1	-	1	1	19	22								44	11.393	0.034
F_2	1	4	11	16	48	79	65	24	15	18	11	6			298	11.444	0.162
BC_{P1}						10	21	17	6	18	16	8	2		98	11.903	0.147
BC_{P2}		6	30	27	26	47	5	2	-	-	1				144	11.067	0.089

Table A-5. Frequency distributions of 232 x 206 generations, location data combined.

Gen.	Upper class limits in hrs of daylight														n	$\bar{x}$	σ^2
	10.4	10.6	10.8	11.0	11.2	11.4	11.6	11.8	12.0	12.2	12.4	12.6	12.8	13.0			
P_1(206)	3	32	17	37	-	3									92	10.705	0.041
P_2(232)						4	1	3	8	17	42	37	26	11	149	12.380	0.106
F_1						49	43	6							98	11.435	0.012
F_2		3	7	13	23	88	56	28	14	22	25	10	1		290	11.562	0.193
BC_{P1}		4	13	22	44	35	17								135	11.136	0.065
BC_{P2}						12	35	35	8	19	22	12	5	1	149	11.889	0.156

APPENDIX B
CHI-SQUARE CONTINGENCY TABLES OF 55 x 232 AND 232 x 206 F_2s

Table B-1. Chi-square contingency table for 55 x 206 at Ft. Pierce.

Class center in hrs daylight	Observed	Expected	Theoretical	$\frac{(O-E)^2}{E}$
10.7	0	0.625	1.25	
10.9	5	6.94	8.87	0.2657
11.1	30	24.52	19.04	
11.3	62	60.59	59.18	0.0328
11.5	18	22.23	26.46	0.8048
11.7	10	13.35	16.69	0.8406
11.9	7	7.13	7.26	0.0024
12.1	6	3.67	1.34	1.4792
12.3	6	3.38	0.75	
12.5	5	4.42	3.84	
12.7	0	1.55	3.10	0.1858
12.9	0	0.32	0.63	
				3.6113

1/2 χ^2 = 3.6113 χ^2 - 7.2226 df = 4 P = 0.10 to 0.05

Table B-2. Chi-square contingency table for 55 x 206 data from both locations combined.

Class center in hrs daylight	Observed	Expected	Theoretical	$\frac{(O-E)^2}{E}$
10.3	1	0.82	0.63	
10.5	4	6.56	9.12	0.0004
10.7	11	8.54	6.08	
10.9	16	20.27	24.53	0.8995
11.1	48	39.93	31.86	1.6309
11.3	79	76.78	74.56	0.0642
11.5	65	71.75	78.49	0.1896
11.7	24	26.23	28.46	0.3183
11.9	15	17.35	19.69	2.2729
12.1	18	12.64	7.27	0.1575
12.3	11	9.76	8.52	
12.5	6	5.45	4.89	
12.7	0	1.55	3.10	0.0004
12.9	0	0.32	0.63	
				6.0110

1/2 χ^2 = 6.011 χ^2 = 12.02 df = 6 P = 0.10 to 0.05

Table B-3. Contingency table for Chi-squares of 232 x 206 at Gainesville.

Class center in hrs daylight	Observed	Expected	Theoretical	$\frac{(O-E)^2}{E}$
10.3	0	0.29	0.58	
10.5	3	4.59	6.18	
10.7	6	4.10	2.19	0.3788
10.9	10	7.53	5.05	
11.1	10	16.45	22.90	2.5290
11.3	31	27.33	23.46	0.5219
11.5	33	33.10	33.19	0.0003
11.7	11	12.27	13.53	0.1315
11.9	7	12.56	18.11	2.4613
12.1	15	12.72	10.44	0.4086
12.3	16	10.50	4.99	
12.5	3	3.10	3.19	
12.7	0	0.31	0.61	1.7200
12.9	0	0.18	0.36	
				8.1514

$1/2\ \chi^2 = 8.1514$ $\chi^2 = 16.3028$ df = 5 P = <0.01

Table B-4. Chi-square contingency table for 232 x 206 at Ft. Pierce.

Class center in hrs daylight	Observed	Expected	Theoretical	$\frac{(O-E)^2}{E}$
10.7	1	1.11	1.22	
10.9	3	5.16	7.32	0.0575
11.1	13	9.77	6.54	
11.3	57	61.40	65.79	0.3153
11.5	23	25.34	27.67	0.2160
11.7	17	13.37	9.74	0.9855
11.9	7	8.59	10.18	0.2943
12.1	7	7.15	7.29	0.0031
12.3	9	6.32	3.64	
12.5	7	4.47	1.94	
12.7	1	1.77	2.54	1.1956
12.9	0	0.49	0.97	
				3.0673

$1/2\ X^2 = 3.0673$ $X^2 = 6.1346$ df = 4 P = 0.20 to 0.10

Table B-5. Chi-square contingency table of 232 x 206 data from locations combined.

Class center in hrs daylight	Observed	Expected	Theoretical	$\frac{(O-E)^2}{E}$
10.3	0	0.61	0.30	
10.5	3	6.29	4.65	0.0061
10.7	7	3.60	5.30	
10.9	13	13.37	13.19	26.37
11.1	23	30.33	26.67	53.33
11.3	88	87.23	87.66	175.32
11.5	56	62.06	59.03	118.06
11.7	28	25.56	27.28	54.56
11.9	14	24.77	19.39	38.77
12.1	22	16.70	19.35	38.70
12.3	25	9.60	17.3	34.60
12.5	10	5.22	7.61	
12.7	1	3.16	2.08	0.0395
12.9	0	1.33	0.67	
				6.0174

1/2 χ^2 = 6.0174 χ^2 = 12.0348 df = 7 P = 0.20 to 0.10

APPENDIX C
CHI-SQUARE CONTINGENCY TABLES OF BACKCROSSES

Table C-1. Chi-square contingency table of (55 x 206) x 55 at Ft. Pierce.

Class center in hrs daylight	Observed	Expected	Theoretical	$\frac{(O-E)^2}{E}$
11.1	0	0.25	0.50	
11.3	10	9.31	8.61	0.0203
11.5	5	6.27	7.55	0.2572
11.7	10	9.60	9.20	0.0167
11.9	4	5.40	6.80	0.3630
12.1	6	4.08	2.16	0.9035
12.3	3	2.01	1.02	
12.5	5	4.83	4.65	
12.7	2	2.88	3.75	0.0008
12.9	0	0.38	0.75	
				1.5615

1/2 χ^2 = 1.5615 χ^2 = 3.123 df = 4 P = 0.70 to 0.50

Table C-2. Chi-square contingency table of (55 x 206) x 206, data from locations combined.

Class center in hrs daylight	Observed	Expected	Theoretical	$\frac{(O-E)^2}{E}$
10.3	0	0.61	1.21	
10.5	6	9.89	13.78	0.0500
10.7	30	21.51	13.02	
10.9	27	31.91	36.82	0.7555
11.1	26	27.16	28.31	0.0495
11.3	47	38.54	30.08	
11.5	5	12.69	20.38	
11.7	2	1.08	0.16	
11.9	0	0	0	0.0908
12.1	0	0	0	
12.3	1	0.5	0	
				1.3958

$1/2\ \chi^2 = 1.3958$ $\chi^2 = 2.7916$ df = 2 P = 0.30 to 0.20

Table C-3. Chi-square contingency table of (55 x 206) x 206 at Gainesville.

Class center in hrs daylight	Observed	Expected	Theoretical	$\frac{(O-E)^2}{E}$
10.3	0	0.68	1.35	
10.5	6	10.96	15.92	0.0143
10.7	28	21.67	15.34	
10.9	15	15.95	16.90	0.0566
11.1	10	8.44	6.87	0.2883
11.3	10	6.39	2.78	
11.5	5	9.92	14.84	0.1052
				0.4644

1/2 χ^2 = 0.4644 χ^2 = 0.9288 df = 2 P = 0.50 to 0.30

Table C-4. Chi-square contingency table of (55 x 206) x 206 at Ft. Pierce.

Class center in hrs daylight	Observed	Expected	Theoretical	$\frac{(O-E)^2}{E}$
10.7	2	2.165	2.33	
10.9	12	13.24	14.48	0.1281
11.1	16	14.49	12.97	0.1574
11.3	37	34.82	32.63	
11.5	0	3.78	7.55	
11.7	2	1.02	0.035	0.0004
12.1	0	0	0	
12.3	1	0.5	0	
				0.2859

1/2 χ^2 = 0.2859 χ^2 = 0.5717 df = 1 P = 0.50 to 0.30

Table C-5. Chi-square contingency table of (232 x 206) x 206 at Ft. Pierce.

Class center in hrs daylight	Observed	Expected	Theoretical	$\frac{(O-E)^2}{E}$
10.7	0	1.07	2.14	
10.9	7	10.39	13.78	1.7357
11.1	31	22.47	13.93	3.2381
11.3	23	25.41	27.81	
11.5	3	4.67	6.33	0.5509
				5.5247

$1/2\ \chi^2 = 5.5247$ $\chi^2 = 11.0494$ df = 1 P = <0.001

Table C-6. Chi-square contingency table of (232 x 206) x 206, location data combined.

Class center in hrs daylight	Observed	Expected	Theoretical	$\frac{(O-E)^2}{E}$
10.3	0	0.56	1.11	
10.5	4	7.88	11.75	0.0993
10.7	13	9.92	6.83	
10.9	22	22.45	22.90	0.0090
11.1	44	37.39	30.77	1.1685
11.3	35	37.98	40.96	0.2338
11.5	17	17.77	18.54	
11.7	0	1.10	2.19	0.1853
				1.6959

$1/2\ \chi^2 = 1.6959$ $\chi^2 = 3.3918$ df = 3 P = 0.50 to 0.30

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BIOGRAPHICAL SKETCH

Christopher W. Deren was born in Illinois in 1949. After completing two years of college in the late 1960s, he spent two and one-half years in Asia and Europe. He then worked in land survey, masonry and as a farrier until he continued his education in 1978. He received his B.S. in agronomy at the University of Arkansas in 1980, and an M.S., also at Arkansas, in 1983, with specialization in cotton breeding.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Kenneth H. Quesenberry, Chairman
Professor of Agronomy

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Earl S. Horner
Professor of Agronomy

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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This dissertation was submitted to the Graduate Faculty of the College of Agriculture and to the Graduate School and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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